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THE HUMERUS OF *CRYPTOTIS COLOMBIANA* AND ITS BEARING ON THE SPECIES' PHYLOGENETIC RELATIONSHIPS (SORICOMORPHA: SORICIDAE)

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The Colombian small-eared shrew, *Cryptotis colombiana* Woodman and Timm, was described from the Colombian Andes in 1993. Its original allocation to the *C. nigrescens* group recently was questioned based on several cranial characters the species appeared to share with some members of the *C. thomasi* group. We review characteristics of the *C. nigrescens* and *C. thomasi* groups, and we describe the humerus of *C. colombiana* and the humerus and manus of *C. medellinia*. The morphology of the humerus joins the suite of characters that supports the hypotheses that *C. colombiana* is not a member of the *C. thomasi* group and that all remaining South American species form a cohesive, definable set that is probably monophyletic.

Key words: anatomy, *Cryptotis*, Insectivora, morphology, osteology

Small-eared shrews, genus *Cryptotis*, are endemic to the New World, extending from southeasternmost Canada and the eastern United States to the Andean highlands of northwestern South America. Recent systematic treatments of the genus have organized most species into 4 definable “species groups” (Choate 1970; Woodman 1996; Woodman and Timm 1993, 1999, 2000): *C. mexicana* group, with 9 species distributed from northeastern Mexico to central Honduras; *C. nigrescens* group, comprising 6 species distributed from southern Mexico to Colombia; *C. parva* group, consisting of at least 2 diagnosable species (*C. orophila* and *C. parva*) that occur from northeastern North America to the Valle Central of Costa Rica; and *C. thomasi* group, with at least 8 species in the northern Andes of South America.

Most South American shrews traditionally have been placed in the *C. thomasi* group (Choate 1970; Woodman 1996,

2002). However, Woodman and Timm (1993) described the Colombian small-eared shrew, *C. colombiana*, from the Central Cordillera of the Colombian Andes, as a member of the mostly Central American *C. nigrescens* group. This designation was based entirely on traditional external and craniomandibular characters because *C. colombiana* was known then from only a single skin and skull, and no postcranial skeleton was available. More recently, the relationship of *C. colombiana* to the *C. nigrescens* group has been questioned and a closer relationship between *C. colombiana* and some members of the *C. thomasi* group inferred (Vivar et al. 1997).

Recent collections on the Central Cordillera of Colombia have yielded additional specimens of *C. colombiana* as well as a poorly documented member of the *C. thomasi* group, *C. medellinia*. These new specimens include portions of the forelimb skeleton that previously were unknown for either species. The external forelimb yields

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suites of characters that aid in understanding the relationships within the genus *Cryptotis* (Choate 1970), and the skeleton of the forelimb, particularly the humerus, has proven especially valuable (Woodman and Timm 1999, 2000). In this study, we review the morphological differences between the *C. nigrescens* and *C. thomasi* groups. We also describe the structure of the humerus of *C. colombiana* and the humerus and manus of *C. medellinia* and show how the morphologies of their respective forelimbs aid us in understanding the relationships of these 2 species.

MATERIALS AND METHODS

Specimens of shrews were collected during a series of biotic inventories in the municipalities of Argelia, Caldas, and Sonsón along the Central Cordillera, Departamento Antioquia, Colombia (C. A. Cuartas-Calle, in litt.; C. A. Cuartas-Calle and M. Peña, in litt.; C. A. Cuartas-Calle et al., in litt.) and as part of a study of food habits of the crab-eating fox, *Cerdocyon thous*, in Antioquia (Delgado-V. 2002). Two specimens of *C. colombiana* were collected using traditional trapping methods. Postcranial material of *C. medellinia* is from an individual found dead along the side of a road and remains (including diagnostic craniomandibular elements) recovered from scat of *Cerdocyon thous*.

Taxonomy of *Cryptotis*, characters, and character polarities follow Woodman (1996, 2002) and Woodman and Timm (1993, 1999, 2000). Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the humerus (Fig. 1) follows Reed (1951). Specimen localities and abbreviations for systematic collections are explained in Appendix I.

RESULTS

Differentiation of *C. nigrescens* and *C. thomasi* groups.—As currently understood, the 4 species groups of *Cryptotis* defined by Choate (1970) and Woodman and Timm (1993, 1999, 2000) are informal groupings of species sharing suites of characters rather than being clades supported by polarized synapomorphies, yet, they have proven useful in working out the taxonomy of the ge-

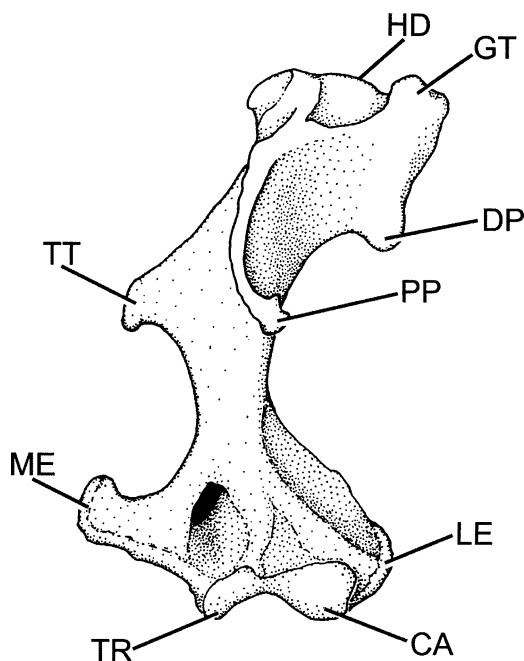


FIG. 1.—Left humerus of *Cryptotis goldmani*, indicating anatomical features mentioned in the text. Abbreviations: CA = capitulum; DP = deltoid process; GT = greater tuberosity; HD = head; LE = lateral epicondyle; ME = medial epicondyle; PP = pectoral process; TR = trochlea; TT = teres tubercle.

nus. The *C. parva* and *C. nigrescens* groups, although superficially appearing closely related, are defined primarily (but not entirely) by plesiomorphic and unpolarized characters. In contrast, the *C. thomasi* and *C. mexicana* groups both possess clearly apomorphic characters, including modifications of the forelimb, that link their respective members phylogenetically (Woodman 1996; Woodman and Timm 1999, 2000). The latter 2 groups also possess characters (e.g., shape of unicuspid and enlargement of processes of the humerus) that indicate a possible close relationship between the 2 groups, and it is likely that the *C. thomasi* group represents a basal branch of the *C. mexicana* group. In addition, their respective memberships are likely to change as additional Central and South American taxa are analyzed and we attain

a more comprehensive grasp of the distributions of characters among these species. Despite the shortcomings of our present level of knowledge of the phylogenetic relationships within the genus, the *C. nigrescens* and *C. thomasi* groups represent 2 very different and clearly definable sets of species.

The complete suite of characteristics defining the *C. nigrescens* group is based on *C. nigrescens* and other Central American and Mexican species for which the postcranial skeleton and fluid-preserved specimens are available. However, the majority of characters have been confirmed for most species. Members of the *C. nigrescens* group are typically small to medium in size for the genus, with mean head-and-body length < 70 mm (the largest specimen, *C. mayensis*, has head-and-body length = 77 mm). Fur is typically shorter (4–5 mm) than in the *C. mexicana* and *C. thomasi* groups, and there is an obvious bare patch marking the positions of the lateral glands in males. Their forefeet are not enlarged, and the foreclaws are neither elongated nor broadened. Metapodials and phalanges of the manus and pes are long and narrow. First through 3rd unicuspid teeth (U1–U3) typically are cone shaped, with a straight or convex posteroventral margin. The anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively high angle. The coronoid process is moderately high to high. The articular process is short, broad, and robust. The lower sigmoid notch is very shallow. The humerus in the *C. nigrescens* group is similar to that of the *C. parva* group: it is long, straight, and narrow (particularly distal to the teres tubercle), with the teres tubercle more proximally located than in either the *C. mexicana* or *C. thomasi* group (but more distally positioned than in *Sorex*); the narrowest portion of the shaft tends to be broader in lateral aspect than in anterior aspect; and the head is more or less rounded. Although most of the processes, particularly the medial epicondyle and teres tubercle,

are prominent relative to *Sorex*, they are small for *Cryptotis*. The lateral epicondyle is unexpanded. The posterior edge of the falciform process of the tibia is not deeply pocketed. The body and the trochlear process of the calcaneum are relatively small. Many of these characters are synapomorphic for *Cryptotis*, but most are plesiomorphic or of uncertain polarity within the genus. In fact, the only clear synapomorphy for the *C. nigrescens* group is that the anterior element of the ectoloph of 1st upper molar (M1) is of approximately the same size as the posterior element. It is possible that the *C. nigrescens* group may prove to be paraphyletic.

Members of the *C. thomasi* group typically are medium to large, with mean head-and-body length > 72 mm; all the named Colombian species have mean head-and-body length > 83 mm. Members of the *C. thomasi* group have longer (about 6–7 mm), more luxuriant fur than members of the *C. nigrescens* group. Unlike most soricines, males of the *C. thomasi* group lack obvious bare patches marking the location of the lateral glands. The forefeet of these shrews are somewhat enlarged, and the foreclaws are elongated (but not broadened). Previously, the skeleton of the feet had not been studied. U1–U3 typically are relatively narrow and concave to very concave on the posteroventral margin. The anterior element of the ectoloph of M1 is reduced relative to the posterior element. The anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively low angle. The coronoid process is low to moderately high. The articular process is high, broad, and less robust than in the *C. nigrescens* group. The lower sigmoid notch is shallow to very shallow. The humerus in the *C. thomasi* group is moderately long, quite robust, and slightly curved; the narrowest portion of the shaft tends to be broader in anterior aspect than in lateral aspect; and the head tends to be dorsoventrally elongate. The processes, particularly the medial epicondyle and teres tubercle,

are more prominent than in the *C. nigrescens* group, and the teres tubercle is more centrally located along the shaft. The posterior edge of the falciform process of the tibia is deeply pocketed. The calcaneum has not been studied. Most of these characters are apomorphic relative to those of the *C. nigrescens* and *C. parva* groups.

Humerus of *C. colombiana*.—External characteristics of the forelimb of *C. colombiana* were described previously (Woodman 1996), and they match the plesiomorphic characters of other members of the *C. nigrescens* group: forefeet are unenlarged, and foreclaws are neither elongated nor broadened. We studied 3 nearly complete humeri from 2 individuals of *C. colombiana*, and, in general, these display the mostly plesiomorphic (for *Cryptotis*) characteristics typical of the *C. nigrescens* group (Figs. 2A–C). The shaft is relatively long, narrow, and straight in anterior aspect, especially distal to the teres tubercle. The narrowest portion of the shaft is broader in lateral aspect than in anterior aspect. The head of the humerus is more or less rounded. The proximal face of the greater tuberosity is broadened with a slight pocket. As in *C. nigrescens*, the pectoral process is high, the teres tubercle is slightly enlarged, the medial epicondyle is slightly enlarged, and the lateral epicondyle is unexpanded; none of these processes is as prominent as in members of the *C. thomasi* group. The position of the teres tubercle along the shaft is similar to that in *C. parva* and *C. nigrescens*, and it is more proximal than in the *C. thomasi* group; the distal edge of pectoral process extends well distal to the teres tubercle.

Humerus and manus of *C. medellinia*.—As in other members of the *C. thomasi* group, forefeet of *C. medellinia* are slightly enlarged, and foreclaws are slightly elongated but not broadened. The humerus has not been described previously for *C. medellinia*, and the manus has not been described for any species within the *C. thomasi* group, making the postcranial mate-

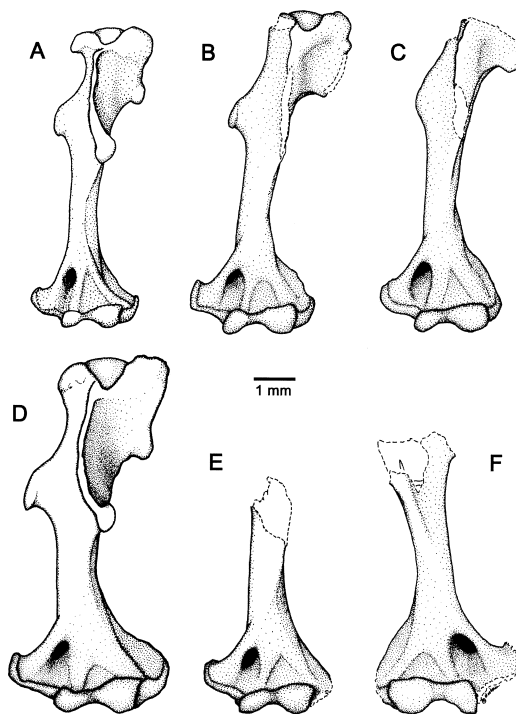


FIG. 2.—Left humeri of A) *Cryptotis nigrescens*, KU 142054; B) *C. colombiana*, MUA 062 and C) MUA 060; and D) *C. thomasi*, FMNH 71027; and E) fragmentary left and F) right humeri of *C. medellinia*, CADV 029 and MUA 061, respectively. Dashed lines represent areas of breakage. Compare also humeri figured in Woodman (2002).

rials described below valuable despite their incompleteness. A right and a left humerus from 2 individuals of different sizes were available for study. Both humeri are broken, so that only the distal portion of the shaft and the distal epiphysis are present, and even these are incomplete, so only some of the major characters can be recorded. In all preserved characters, as well as overall shape, the humeri match most closely those of other members of the *C. thomasi* group (Figs. 2D–F): the shaft is broader in anterior aspect than in lateral aspect, the medial epicondyle is elongate, and the lateral epicondyle is expanded.

Of secondary interest, the humeri share a gross structural similarity in cross section,

visible along the broken portion of the shaft, to avian long bones. Externally, there is a thin layer of compact bone forming the cortex. Internally, the shafts of the bones are mostly hollow, with a few thin struts supporting the walls. The lack of internal spongy bone may be a result of the small size of shrews and the resulting low level of stress on the skeleton, or possibly the struts are spongy bone but on a shrew-sized scale. Despite the superficial resemblance, the cortex of avian bones is distinct histologically, being more complex than that of soricid bones (Foote 1916).

The metacarpals of *C. medellinia* are relatively long and broad (Fig. 3) compared with those of *C. parva* and *C. nigrescens*, in which these bones are long but quite narrow. The broadening is similar to that observed among less-derived members of the *C. mexicana* group (Woodman and Timm 1999). However, the proximal phalanges of *C. medellinia* are relatively long and narrow as in *C. parva* and *C. nigrescens*. In the *C. mexicana* group, the proximal (and middle) phalanges exhibit shortening and broadening along with the metacarpals; this is particularly evident in more derived species, such as *C. goldmani*. Metacarpal V of *C. medellinia* is more strongly curved (laterally concave) than in any species of *Cryptotis* for which the manus has been studied. The distal tip of the proximal phalanx of digit V extends distinctly distal to the tip of metacarpal IV, rather than the 2 terminating at approximately the same position (as in *C. parva*). Carpals remain unknown.

DISCUSSION

Cryptotis colombiana possesses external and craniomandibular characteristics that define the *C. nigrescens* group, and based on these characteristics, it was described as a member of this group (Woodman and Timm 1993). Vivar et al. (1997), however, reached a different conclusion, suggesting that *C. colombiana* be removed from the *C. nigrescens* group and that the *C. thomasi* group be redefined to consist only of *C.*

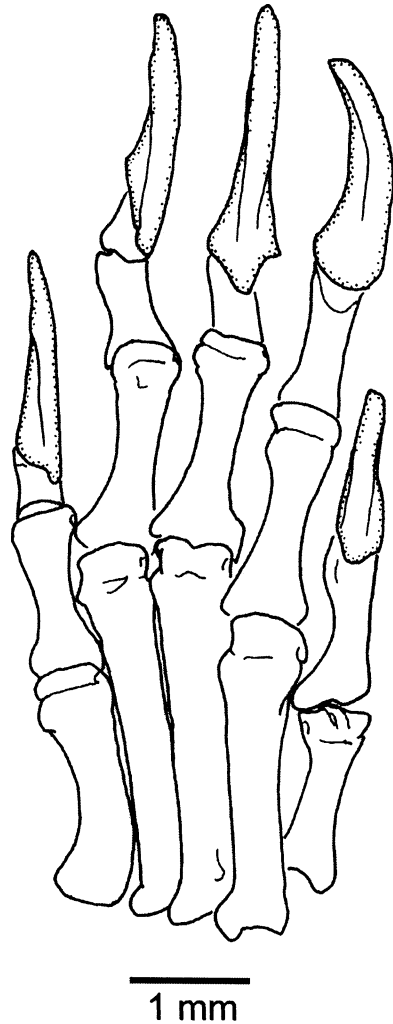


FIG. 3.—Metacarpals and phalanges of the left manus of *Cryptotis medellinia* (CADV 029). Distal elements with stippled borders are claw sheaths.

thomasi and possibly *C. medellinia*. Confusion about the relationships of *C. colombiana* perhaps resulted from the use of several characters, most of which originally were used to distinguish *C. colombiana* from other members of the *C. nigrescens* group (rather than establish it as a member of this group):

- 1) The presence of a very large foramen on the posterior edge of the tympanic process of the petromastoid clearly and easily

distinguishes *C. colombiana* within the *C. nigrescens* group. This character is problematic because a very large foramen also is present on the tympanic processes of 2 members of the *C. thomasi* group: *C. thomasi* and *C. medellinia*. Foramina of various sizes (but never as large as in *C. colombiana* or *C. thomasi*) also are present in *C. meridensis* and several other Andean taxa. Among Central American and Mexican species, the foramen is always minute or absent.

2) A high, more robust anterior process of the petromastoid distinguishes *C. colombiana* within the *C. nigrescens* group. This character is more variable within many species than the previous character, and the anterior process of the petromastoid often is broken, making it difficult to determine its size. Within and among species of the *C. thomasi* group, the height and width of the process is extremely variable and therefore does not appear to be particularly useful for either defining the group or distinguishing species within the group.

3) A shallow lingual notch between the facets of the articular condyle also identifies *C. colombiana*. As noted above, the articular condyle of the mandible in the *C. nigrescens* group tends to be short, broad, and robust, whereas that in the *C. thomasi* group tends to be tall, broad, and less robust. The articular condyle of *C. colombiana* is particularly robust, and the ascending ramus of the condyle is so broad as to nearly fill the region between the articular facets. Although not delicate, the articular condyle in the *C. thomasi* group is not nearly so broad, and we have not seen any member of this group comparable with *C. colombiana* in this regard.

4) A short articular condyle aids in distinguishing members of the *C. nigrescens* and *C. parva* groups from members of the *C. mexicana* and *C. thomasi* groups. As partly noted for the last character, the articular condyle in the former 2 groups tends to be short, broad, and robust, and it is tall,

broad, and less robust in the latter 2 groups. *C. colombiana* conforms morphologically with the *C. nigrescens* group; all other Andean species of shrews that we have inspected match more closely the shape described for the *C. thomasi* group.

A broad anterior process of the petromastoid and a shallow lingual notch on the articular condyle are autoapomorphies that are uninformative phylogenetically. A short articular condyle is characteristic of the *C. nigrescens* group but plesiomorphic for the genus and, therefore, not useful for determining evolutionary relationships. In the absence of other data, a large foramen on the tympanic process would serve as a synapomorphy linking all those taxa that possessed it, thus marking *C. colombiana*, *C. thomasi*, and *C. medellinia* as sister taxa. However, even if all 4 characters suggested such a linkage, there exist a greater number of external and craniomandibular characters defining the *C. thomasi* group (see above) that *C. colombiana* lacks. Instead, *C. colombiana* possesses the synapomorphic morphology and the other, generally plesiomorphic characters that mark the *C. nigrescens* group.

The morphology of the humerus of *C. colombiana* is nearly identical with that of other members of the *C. nigrescens* group, and this fact provides additional support for the hypothesis that *C. colombiana* is not a member of the *C. thomasi* group. Similarly, the morphology of the humerus of *C. medellinia* supports its allocation to the *C. thomasi* group. The distinctiveness of the humeri of the 2 species attests to both the differentiation of this element between the 2 groups and the relative conservatism of its form within each group. That these 2 forelimb morphologies represent distinct lineages differentially adapted for survival in a common habitat makes sense ecologically. In some communities of sympatric soricids, body size reflects foraging mode. Larger species (such as members of the *C. thomasi* group) are soil foragers that tend to take

larger prey, such as earthworms, whereas smaller species (members of the *C. nigrescens* group) include a greater proportion of smaller, surface-dwelling invertebrates in their diets (Churchfield 1991; Churchfield and Sheftel 1994). Larger size has been hypothesized to reflect the physical requirements of foraging either on larger prey or deeper in the soil horizon (Churchfield and Sheftel 1994). Apomorphic characters of the forelimb in the *C. thomasi* group may include adaptations that enhance such foraging activities in Andean environments.

RESUMEN

La musaraña Colombiana, *Cryptotis colombiana* Woodman y Timm, fue descrita de los Andes Colombianos en 1993. La ubicación de esta especie al grupo *C. nigrescens* fue cuestionada al tener en cuenta varios caracteres craneales que la especie pareció compartir con algunos miembros del grupo *C. thomasi*. Revisamos las características de los grupos *C. nigrescens* y *C. thomasi*, y describimos el húmero de *C. colombiana* y el húmero y la mano de *C. medelliniana*. La morfología del húmero junto a los caracteres externos y craneomandibulares soportan la hipótesis que *C. colombiana* no es un miembro del grupo *C. thomasi* y que las restantes especies Suramericanas forman un grupo definible el cual es probablemente monofilético.

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APPENDIX I

Specimens figured.—Abbreviations for systematic collections: CADV = collector Carlos A. Delgado-V., uncataloged material to be de-

posited in Museo de la Universidad de Antioquia; FMNH = The Field Museum, Chicago, Illinois; KU = University of Kansas Natural History Museum, Lawrence, Kansas; MUA = Museo de la Universidad de Antioquia, Medellín, Colombia; USNM = National Museum of Natural History, Washington, D.C.

Cryptotis colombiana.—COLOMBIA: Antioquia: Corregimiento San Antonio de Prado, 2,100–2,800 m, Municipio de Medellín (MUA 060, 062).

Cryptotis medellinia.—COLOMBIA: Antioquia: Municipio de Santa Rosa de Osos, 3,000 m (MUA 061); Alto San Luis, 2,600–2,800 m, Reserva Ecológica San Sebastián–La Castellana, Municipio de El Retiro (CADV 029).

Cryptotis nigrescens.—COSTA RICA: Puntarenas: Monteverde, Cerro Amigos, 1,760 m (KU 142054).

Cryptotis thomasi.—COLOMBIA: Cundinamarca: San Francisco de Bogotá, 3,000 m (FMNH 71027).